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TEMPORAL FLUCTUATION OF PHYTOPLANKTONIC CHLOROPHYLL *A* AND PRIMARY PRODUCTION IN A TURBID FLOODPLAIN LAKE OF THE RIVER PARANA (ARGENTINA)

FLUCTUACIONES TEMPORALES DE LA CLOROFILA A *Y DE LA PRODUCCION PRIMARIA FITOPLANCTONICA EN UNA LAGUNA TURBIA DE LA LLANURA DE INUNDACION DEL RIO PARANA (ARGENTINA)*

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ABSTRACT

The seasonal pattern of vertical distribution of chlorophyll *a* and primary production was studied in a floodplain lake of the Lower Paraná River from May 1995 to May 1996. No stable stratification was observed during the study period for lake Montiel, a typical turbulent and shallow lake. Chlorophyll *a*, mainly regulated by the hydrological regime and by seasonal changes in temperature and light, attained concentrations which exceeded 10 $\mu g\ l^{-1}$ during late spring and early summer. Severe dilution occurred during high water level periods while light limitation in the water column was observed for the driest periods due to sediment resuspension from the bottom. Gross primary production per unit area ranged from 0.114 $g\ m^{-2}h^{-1}$ to 1.235 $g\ m^{-2}h^{-1}$. In general, production sharply declined with depth because of light attenuation by suspended solids. Net production appeared to be limited by light penetration and by hydrological mechanisms which exerted a significant influence on the limnological parameters of the lake.

KEYWORDS: Floodplain lake, primary production, chlorophyll *a*, phytoplankton, Paraná River, Argentina.

RESUMEN

En el presente trabajo se analiza la variación estacional de la distribución vertical de clorofila *a* y de la producción primaria fitoplanctónica de una laguna de la llanura de inundación del Paraná Inferior. Los muestreos abarcaron un ciclo anual, entre mayo de 1995 y mayo de 1996. Debido a la frecuente mixis de las aguas, no se evidenció ninguna estratificación vertical estable. La concentración de clorofila *a* estuvo regulada principalmente por el régimen hidrológico y por las variaciones estacionales de luz y temperatura. Las máximas concentraciones fueron registradas hacia fines de la primavera y comienzos del verano, con valores superiores a 10 $\mu g\ l^{-1}$. En los períodos de aguas altas se observó una marcada dilución, mientras que en las fase de aguas bajas se evidenció cierta limitación por luz debido a la resuspensión de los sedimentos. La producción primaria bruta por área fluctuó entre 0.114 $g\ m^{-2}\ h^{-1}$ y 1.235 $g\ m^{-2}\ h^{-1}$. En general se detectó una brusca disminución de la producción primaria en función de la profundidad debido a la gran cantidad de sólidos en suspensión. La producción neta de esta laguna estaría limitada por la disponibilidad de luz y por la dinámica hidrológica.

PALABRAS CLAVES: Laguna, llanura de inundación, producción primaria, clorofila *a*, fitoplancton, río Paraná, Argentina.

INTRODUCTION

The Paraná River hydrological regime regulates most of the floodplain lakes physical and chemical characteristics. Thus, the bioproductive mechanisms of the water bodies of the alluvial valley are also influenced by the hydrological fluctuations (Bonetto & Wais, 1987). As it was discussed by Junk *et al.* (1989), the flood pulse is considered to be the principal driving force for the existence, productivity and interactions of the biota in these ecosystems. Several studies on phytoplankton have been conducted in South American floodplain lakes (Bonetto *et al.*, 1994;

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García de Emiliani, 1993; Zalocar de Domitrovic, 1990, 1992). Detailed studies on primary production of the different type of Amazonian waters were carried out by Schmidt (1976, 1982), Fisher (1978), Fisher *et al.* (1988), Fittkau *et al.* (1975) and Rai & Hill (1984). The Orinoco River, its tributaries and related lakes have been surveyed by Lewis (1988) and Lewis & Weibezahn (1976) originating comprehensive works on the energy flow of these systems. In contrast with the Amazon, the Paraná lakes were scarcely studied. Most investigations refer to the Paraná River on its Upper and Middle reaches and specially to its main channel (Bonetto *et al.*, 1979, 1982, 1983). In relation to the primary production of the floodplain shallow lakes, Perotti de Jorda (1977) carried out a study on phytoplankton biomass and production in Los Matadores pond (Middle Paraná). Later on, Carignan & Planas (1994) compared three approaches for the recognition of nutrient and light limitation of productivity in different lakes of the Paraná floodplain.

The Lower Paraná has a large floodplain, which extends over the left side of the river valley. The main course is divided into several channels enclosing a complex formation of low islands. The present study was conducted on a shallow and turbid lake located on the fringing floodplain opposite the city of Villa Constitución, Argentina (Lake Montiel).

The main objectives of this study were to determine the seasonal pattern of vertical distribution of chlorophyll *a*, gross primary production and community respiration in a floodplain lake of the Lower Paraná River and to evaluate factors controlling both processes.

STUDY SITE

The study was carried out in a floodplain shallow lake of the Lower Paraná River (Lake Montiel), which is located in the left margin of the main course (33°15'S; 60°30'W) (Fig. 1).

According to the classification proposed by Drago (1990), Lake Montiel can be considered as a typical pond with "indirect connection" to the river, since it is communicated with the River Paraná by a stream. Nevertheless during periods of high river discharge, its connection is direct. As other floodplain waterbodies of the Paraná, Lake Montiel has an alluvial origin, formed by a combination of erosion and sediment deposition. These lakes are annually filled during the rising water phase as a consequence of the river water inflow. At falling stages, the surplus pond water flows back into the river. The strong influence of the seasonal fluctuations of the Paraná level on the hydrological characteristics of the floodplain lakes has also been well documented by García de Emiliani (1993). Following Junk's criterion (1983), this kind of water body can be considered as intermediate between a closed lake as accumulating system and a river as a discharging one.

Lake Montiel has an area about 5.4 km^2, which is subject to a great variation due to the nature of this water body. Although the morphometric features of the lake have not been studied, observations carried out by Prefectura Naval Argentina from Villa Constitución (Santa Fe Province), establish that the maximum depth would be higher than 10 meters. The maximum depth at the incubation site for the study period varied between 3 and 6 meters.

METHODS

The study comprised one year of monthly samplings, between 24 May 1995 and 14 May 1996. A sampling site was established in the pelagic zone of the lake where depth was approximately 4-6 meters. Sample collections and incubations were performed at five depths, encompassing completely the euphotic zone of the lake at regular intervals from the surface up to a depth below Z_{secchi} x 3 level. Water samples at the different depths were obtained by means of a peristaltic pump. Water temperature, pH and conductivity were measured with Hanna HI 8314 and HI 8033 portable sensors, and transparency with a Secchi disk. Dissolved oxygen was estimated according to Winkler method (APHA, 1975); the titration end point was detected visually with starch indicator (precision ± 0.2 mgl^{-1}). Water samples for chemical analyses were also collected at each depth, and filtered through Whatman GF/F filters. Soluble reactive phosphorus (SRP) was analysed according to the stannous chloride method (APHA, 1975) and NO_3-N was determined following the spongy cadmium technique (Mackereth *et al.*, 1978). Total phosphorus (TP) was determined in non filtered samples after an acid digestion by the stannous chloride method.

Suspended solids concentrations were obtained filtering the water samples through predried glassfibre filters (Whatman GF/F); dry mass was determined according to APHA (1975).

Water samples for chlorophyll *a* analyses were also filtered through Whatman GF/F. Filters were stored at -20°C, and then pigments were extracted with hot ethanol (60-70°C). The extracts were centrifuged and chlorophyll *a* (corrected for phaeopigments) was measured by spectrophotometry before and after acidification with HCl (0.1 N). Chlorophyll *a* concentrations were calculated using the equations given by Marker *et al.* (1980).

Phytoplankton primary production was estimated by means of the oxygen light-dark bottle technique, following recommendations given by Dokulil (1984). Bottles were suspended by means of the dispositives proposed by Boltovskoy & Velez (1983/4), and incubated for 5-6 hours between 10:00/11:00 - 16:00/17:00 h. Incident irradiance was measured each half an hour during incubation with a quantum sensor (Photovolt Corp.). Average irradiance at each incubation depth was estimated assuming that at Secchi disk depth the irradiance is about 20% that of the surface (Golterman, 1975). Since the water level of lake Montiel is directly regulated by the discharge of the River Paraná, the daily records of the water level in the river at this point (Villa Constitución) recorded by Prefectura Naval Argentina were used.

Two way analyses of variance with physical and chemical variables were used to test the hypothesis of vertical homogeneity. Correlation analyses between biotic and abiotic variables were performed using Spearman's rank correlation procedure.

RESULTS

a) Physical and chemical features

The water level of the Paraná River at Villa Constitución varied between 1.45 and 3.86 meters. The flood peaks were registered in May 1995 and 1996, a minor increase was observed during November (Fig. 2).

The analyses of variance revealed that the mixing of the water column was complete. while significant differences were observed among the sampling dates ($p<0.001$).

Temperature ranged from 9.9 to 25.4°C. Differences among the five depths were usually less than 1°C, thus revealing the absence of a thermocline. Mean conductivity was of 100 $\mu S\ cm^{-1}$ with the lowest figure in August 1995 (59.1 $\mu S\ cm^{-1}$) and maximum in November 1996 (173 $\mu S\ cm^{-1}$). Secchi transparency was low throughout the year varying between 15 and 48 cm. Transparency was least during drought periods and relatively high during the flooding season. Water level of the main course influenced the content of suspended solids in the lake, which on time determined the transparency values (Fig. 3). Light penetration profiles showed a significant light attenuation with depth as a consequence of the high content of suspended solids. In general terms, the mixing depth (Zm) exceeded 4-5 times the euphotic zone. Light penetration was influenced by river discharge, registering the highest $Z_{0.5IK}$ during periods of high water level in the lake.

Soluble reactive phosphorus (SRP) concentrations were maximum in summer (> 50 $\mu g\ l^{-1}$), and exhibited the lowest values during high water periods. Total phosphorus (TP) ranged between 9 and 245 $\mu g\ l^{-1}$ with a mean of 95.4 $\mu g\ l^{-1}$. In the same way as SRP, TP was strongly influenced by water level (Fig. 4). Nitrate ($N-NO_3$) mean concentrations for each sampling date ranged from 6.1 to 309.2 $\mu g\ l^{-1}$ and averaged about 181.35 $\mu g\ l^{-1}$(Fig. 5). No seasonal pattern was observed.

b) Chlorophyll *a* and primary production measurements

Chlorophyll *a* concentrations were very low from May to August 1995 (less than 5 $\mu g\ l^{-1}$); from September on a clear increasing pattern was observed, reaching a maximum of 22.5 $\mu g\ l^{-1}$ in November. Later on, concentrations decreased up to values similar to those registered at the beginning of the study (Fig. 6). Mean chlorophyll *a* and chlorophyll *a* per unit area were inversely correlated to river water level ($r = -0.66$, $p<0.01$ and $r = -0.49$, $p< 0.06$) due to the dilution effect. On the other hand, a direct correlation was found between mean chlorophyll *a* and temperature ($r = 0.56$, $p<0.05$) and with nutrients, being more significant the relation with TP ($r = 0.73$, $p<0.01$). Chlorophyll *a* shows an increasing trend with enhanced mean incident light (Fig. 7), revealed by a significant correlation ($r = 0.59$, $p< 0.05$). Mean gross primary production (GPP) for each sampling date varied between 1085 and 133 μg O_2 $l^{-1}h^{-1}$, corresponding these values to May 1995 and May 1996 respectively. With the exception of the figures recorded for May 1995 and June 1995, mean GPP showed a temporal pattern similar to chlorophyll *a*, with a clear maximum in spring (Fig. 8). Mean community respiration (CR) was maximum in May 1995 during high water level (1910 μg O_2 $l^{-1}h^{-1}$), whereas the lowest value was registered at the beginning of August (8.6 μg O_2 $l^{-1}h^{-1}$). GPP per unit area ranged from 0.114 g O_2 $m^{-2}h^{-1}$ to 1.235 g O_2 $m^{-2}h^{-1}$, CR per unit area between 0.09 g O_2 $m^{-2}h^{-1}$ and 2.29 g O_2 $m^{-2}h^{-1}$ (Table I).

In general, maximum production was found at the surface or at the first 40 cm, declining sharply with depth because of light attenuation by suspended solids. Thus, GPP per unit area showed a significant correlation with $Z_{0.51K}$ ($r=-0.52$, $p<0.05$). Regarding the vertical profiles of GPP and CR for each sampling date (Fig. 9), in general NPP is confined to the first 40-60 cm depth.

The P:R ratio (GPP:CR) varied between 0.54 (May 1995) and 2.61 (July 1995), with an average of 1.47. The lowest figures coincided with periods of high river discharge and flooding.

The ratio of production per unit biomass of the producer (GPP: milligram of chlorophyll *a*) per unit time estimated for Lake Montiel showed relatively high values, probably due to the low pigment concentration found for some sampling dates. Since the oxygen technique is not so precise as the C_{14} method, in the estimation of the photosynthetic capacity we only consider data corresponding to dates when mean chlorophyll *a* was higher than 5 μg l^{-1}. Thus, figures ranged from 20 to 50 mg O_2 (mg chl *a*) h^{-1}. On the other hand, if the quotients are based on the NPP, their values varied from 11 to 42 mg O_2 (mg chl *a*) h^{-1}. Considering only these sampling dates, daily GPP per unit area varied between 1.14 and 3.65 g O_2 $m^{-2}day^{-1}$.

DISCUSSIONS AND CONCLUSIONS

Lake Montiel is a typical turbulent, turbid shallow lake lacking stable stratification. This was evidenced from the homogeneous distribution of physical and chemical parameters in the incubation profile. Suspended solid concentration, as well as Secchi disk values, were comparable to other turbid systems (Padisák & Dokulil, 1994; Yin *et al.*, 1996). Due to its direct connection with the Paraná River, water retention time is strongly influenced by river discharge. In this sense, Lake Montiel exhibits a similar behaviour as other floodplain lakes (Drago, 1990).

According to the nutrient concentrations and following Lee *et al.* (1981), the lake can be considered as eutrophic. In general terms, in lowland rivers with large catchment areas, the nutrient input from the watershed is likely to exceed the requirements of primary production (Descy *et al.*, 1987). The high TP figures registered during low water level periods are probably related to the resuspension of sediments from the bottom due to the shallowness of the lake. Soluble reactive phosphorus (SRP) and nitrate concentrations are within the range reported for another marginal lake of the Lower Paraná River (Bonetto *et al.*, 1994). In this study, the authors speculate that nitrogen limitation may occur in this system. In the same way, Carignan & Planas (1994) indicated that in some floodplain lakes surveyed in the Middle Paraná, planktonic primary production can be limited by nitrogen and/or light.

Algal growth, measured by means of chlorophyll *a*, is mainly regulated by the hydrological regime and seasonal changes in temperature and light. Thus, maximum chlorophyll *a* concentrations were registered for late spring and early summer with adequate light intensities and medium water levels. Moreover, the high nitrate concentrations which are related to the inputs from the river during the filling phase of the lake, may also explain the November chlorophyll *a* peak. The influence of the river discharge on phytoplankton development in the lake is evident during the high water phase when algal populations are severely diluted. During these periods the hydraulic retention time strongly decreases. In this sense, Van den Brink (1994) discussed the influence of the connectedness of the floodplain lakes to the main channel on the development of its plankton communities. The direct connection of Lake Montiel to the river during floods explains the fact that changes in phytoplankton abundance are immediate to the increase in water discharge. On the other hand, during the driest period (late summer), even though irradiance was high, pigment concentration was low due to light limitation by turbidity in the water column.

According to chlorophyll *a* concentrations, Lake Montiel could be characterised as a typical meso to eutrophic system, reaching values higher than 10 µg l^{-1} in spring time. In general, our chlorophyll *a* values are higher than those reported for the Paraná River at its Upper reach (Thomaz *et al.*, 1992), and similar to those registered by Perotti de Jorda (1977) for a floodplain lake of the Middle Paraná. As Thomaz (1991) in Thomaz (1992) and Bonetto *et al.* (1969) referred to, phytoplankton in water bodies of the alluvial valley reaches substantial densities, with concomitant high chlorophyll *a* concentrations.

The vertical distribution of chlorophyll *a* in the euphotic zone is fairly homogeneous due to the continuous mixis of the lake. Contrarily, primary production shows a profile typical of turbid and eutrophic systems, where a sharp decline with depth occurs. The high turbidity limits the euphotic layer and condenses the productive zone to one meter or less. Only during periods of fairly high transparency, the net production exceeds the first meter. The same pattern was described by Perotti de Jorda (1977). Nevertheless, it is important to stress that in turbulent water bodies primary production incubation should simulate the algal transport by turbulent flow (Uehlinger, 1993).

As illustrated in Fig. 8, community production and respiration are regulated by the hydrological changes and by temperature. At the beginning of the study CR is enhanced after an important flood, probably by an increase of allochtonous matter and a consequent bacterial metabolism. Thus the lowest P:R quotient was observed at this moment. The important role of the organic matter from adjacent floodplains on the CR has been reported by Uehlinger (*op. cit.*). We hypothesise that the high GPP observed in spite of the low chlorophyll *a* values, could correspond to the picoplanktonic fraction. From June to October a net primary production was observed as a consequence of low CR in winter. In November, with a new water peak, CR increased and once again the P:R quotient was less than one. From December to March, GPP decreased following high turbidity. A second period of net production was observed when light conditions improved (March to May). Finally, with a new flooding period (May 1996) CR increased and a new heterotophic phase was observed. So, net production in this system seems to be limited by light penetration and by hydrological mechanisms which exert a significant influence on the limnological parameters of the lake. According to Talling (1971), net photosynthesis may be negative when the mixing depth exceeds 4-5 times the euphotic zone. This condition was repeatedly registered in Montiel Lake where turbulence together with the morphometric characteristics (shallowness, relatively short residence time) severely limit the euphotic zone. In general terms, and considering an annual cycle, net production of the whole water column is restricted to short periods. The suppression of production by low transparency has been observed throughout the Lower Orinoco System (Lewis, 1988).

The high values yielded when estimating the photosynthetic capacities, probably obey to the low sensibility of the oxygen technique for low chlorophyll *a* concentrations. Nevertheless, when higher pigment concentrations were registered the ratio of production per chlorophyll *a* showed elevated values. The high efficiencies observed are typical of turbid systems where light limitation is one of the main factors regulating phytoplankton growth.

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TABLE I: Gross primary production (GPP) and community respiration (CR) per unit area (g O_2 m^{-2} h^{-1}). GPP/CR rates and mean chlorophyll *a* (µg l^{-1}).

	GPP	CR	GPP/CR	Chlorophyll *a*
May 1995	1.235	2.295	0.54	1.16
June	0.546	0.211	2.59	1.74
July	0.452	0.173	2.61	4.21
September	0.207	0.134	1.54	8.04
October	0.282	0.139	2.03	6.82
November	0.325	0.471	0.69	12.48
December	0.365	0.381	0.96	9.87
March 1996	0.114	0.143	0.80	2.76
April	0.212	0.099	2.15	2.75
May	0.241	0.293	0.82	1.45

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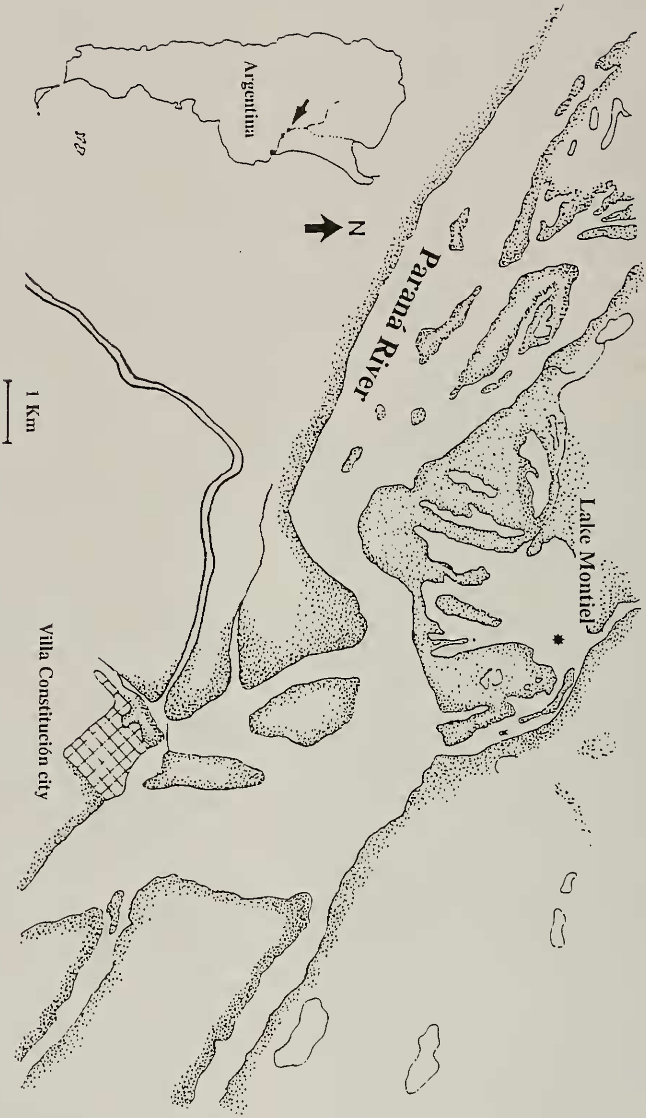

FIG. 1. Map of Lake Montiel indicating the sampling site.

FIG. 2. Water level annual curve for the Paraná River at Villa Constitución.

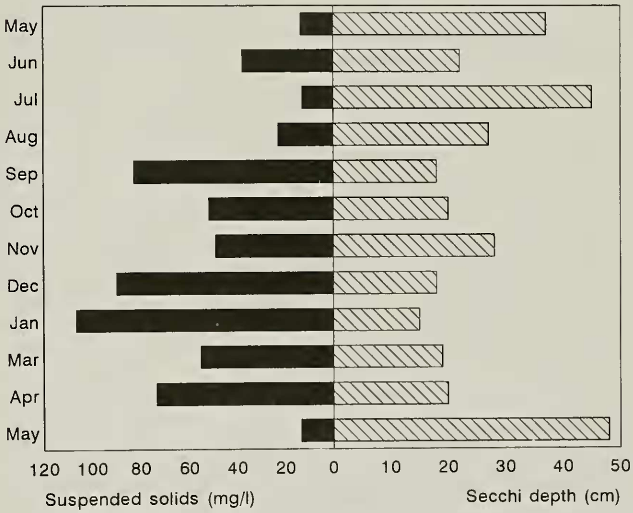

FIG. 3. Monthly fluctuation of the suspended solids concentration and the Secchi disk depth.

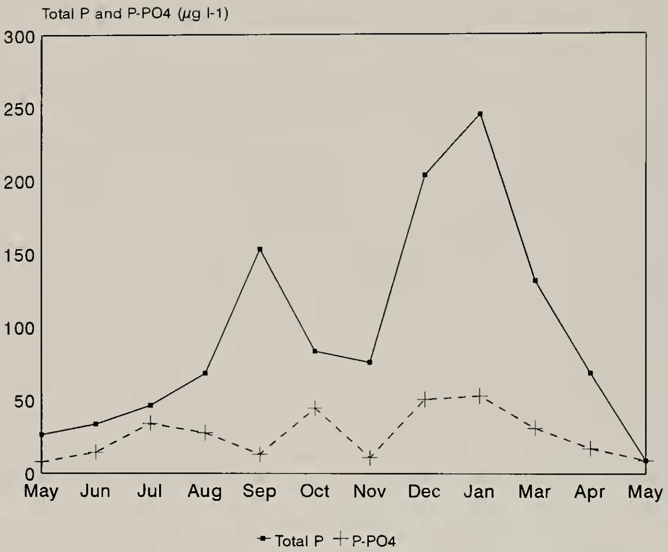

FIG. 4. Total and soluble reactive phosphorus concentrations corresponding to mean values of the water column for the study period.

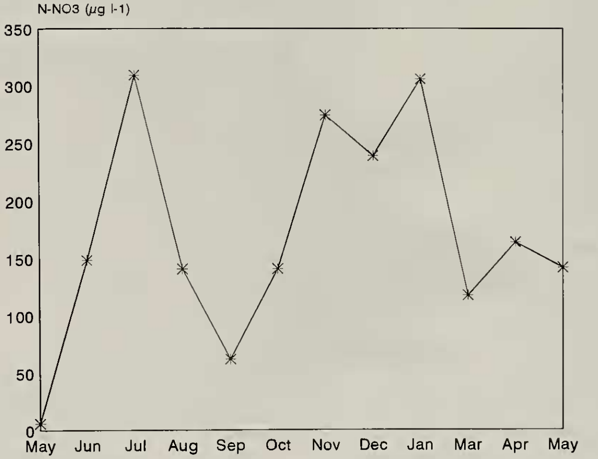

FIG. 5. Mean nitrate concentrations of the water column during the study period.

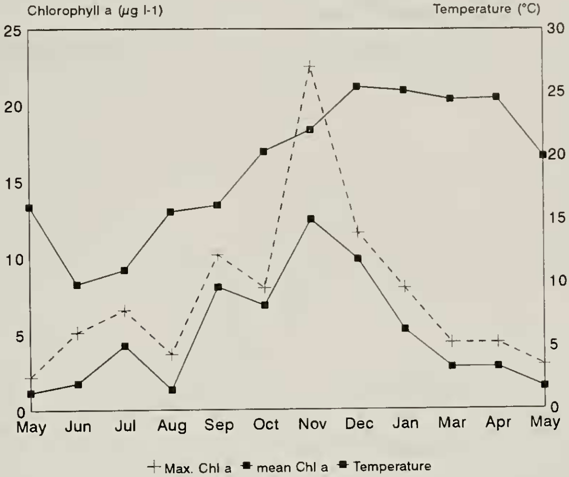

FIG. 6. Mean and maximum chlorophyll *a* concentrations and mean temperature of the incubation profile for each sampling date.

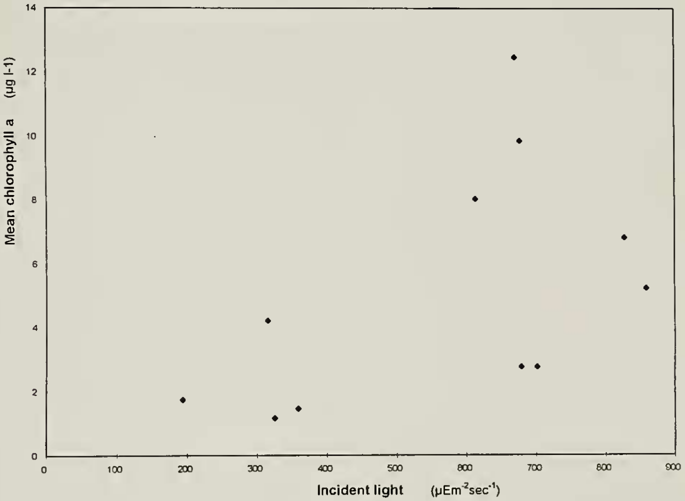

FIG. 7. Correlation between mean incident light and chlorophyll *a* concentrations during the study period.

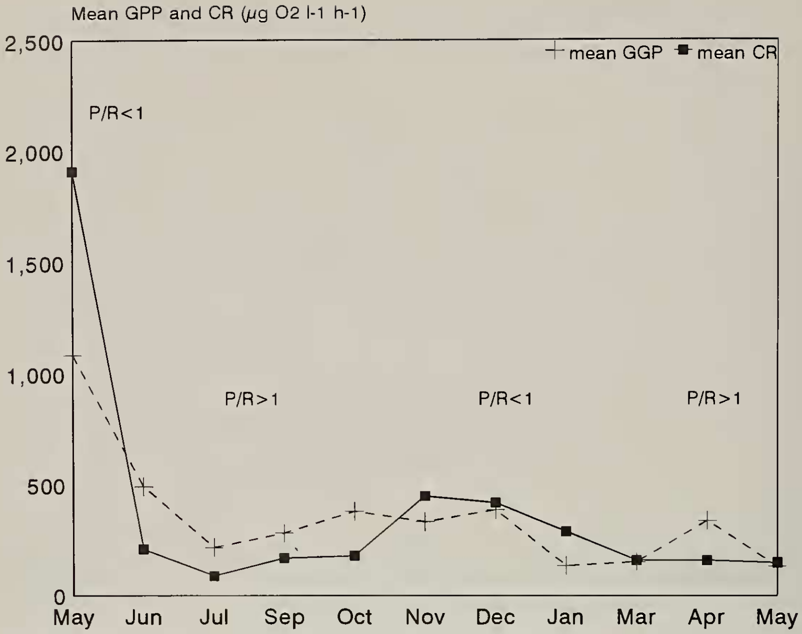

FIG. 8. Mean gross primary production and community respiration in Lake Montiel from May 1995 to May 1996.

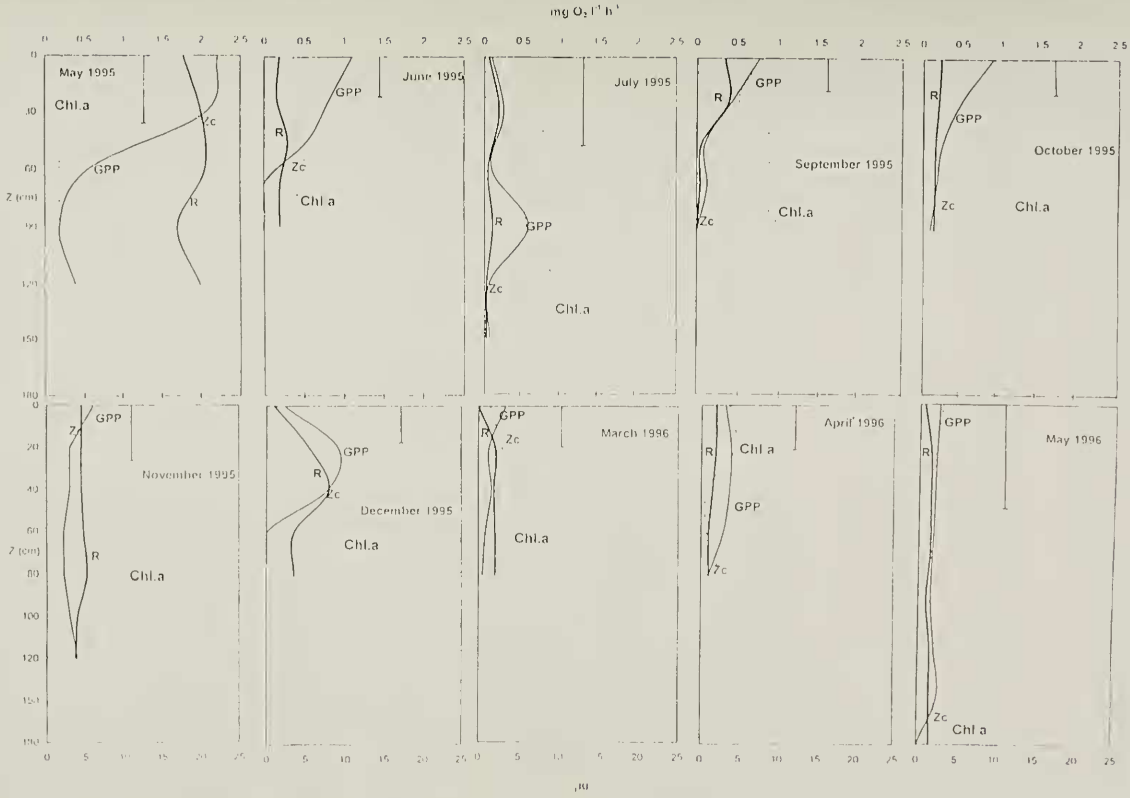

FIG. 9. Depth profiles of chlorophyll *a*, primary gross production and respiration of Lake Montiel. Secchi depth and the compensation depth (Zc) are indicated for each month.